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ORIGINAL ARTICLE

Fossil cladoceran record from Lake Piramide Inferiore (5067 m asl) in the Nepalese Himalayas: biogeographical and paleoecological implications

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ABSTRACT

We investigated 2500 years of community succession in Cladocera from the sediments of a mountain lake (Lake Piramide Inferiore) located in the Khumbu Valley close to Mt. Everest in the Nepalese Himalayas. Our objective was to determine late Holocene changes in cladoceran species composition and abundance in a biogeographical context and with respect to previous proxy-based paleolimnological data (algal pigments and organic content). The results suggested that cladoceran fauna of Lake Piramide Inferiore was species-poor and dominated by Chydorus *cf.* sphaericus *throughout the sequence. The sediment profile recorded the occurrence of* Alona guttata *type individuals, which were attributed to* Alona werestschagini *Sinev 1999 based on their morphology and the species' current distributional range, and this was the first record of its presence in the Himalayas. In addition, a periodic long-term succession of melanic* Daphnia (Ctenodaphnia) fusca *Gurney, 1907 and non-melanic* D. (Daphnia) dentifera *Forbes 1893 was observed in the sediments. The millennia-long cladoceran community changes, although subtle due to the* C. *cf.* sphaericus *dominance, were in general agreement with the previous proxy-data of lake productivity following the regional paleoclimatic development and apparently partly driven by bottom-up mechanisms. The periodic occurrence and success of* D. fusca *and* D. dentifera *throughout the late Holocene in Lake Piramide Inferiore, combined with the knowledge of their phenotypic properties* (i.e.*, carapace melanization*) *and previous investigations on their contemporary and past distribution in Khumbu Valley, suggested that they may have responded to altered underwater UV radiation regimes. Furthermore, they may have even periodically excluded each other subsequent to changes in the underwater UV environment. The results indicated the usefulness of fossil cladoceran analysis as a tool in biogeographical research, since the occurrence of species in space and time can be observed through sediment records and taxonomic identity of the remains may be resolved with the help of regional faunal distribution.*

Key words: Alona werestschagini, Ctenodaphnia, *Khumbu Valley, Late Holocene, Mountain lakes, UV response.*

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INTRODUCTION

Mountain regions cover about one fifth of the Earth's continental areas, these regions are extraordinary features of the global landscape (Meybeck *et al.*, 2001), and they play a major role in abiotic hydrological and climatic processes, as well as in biogeographical phenomena. The general environmental characteristics in mountainous regions across the planet are relatively similar due to the altitudinal gradient, for example having cold climate, snow and glacier covers, steep slopes, thin soils and atmosphere, and prevailing high ultraviolet radiation (Ohrendorf *et al.*, 2000; Sommaruga, 2001; Thompson *et al.*, 2005). These characteristics affect and structure high altitude ecosystems, such as alpine freshwater lakes, and make them highly vulnerable to anthropogenic environmental changes, such as global warming (Sommaruga and Psenner, 2001; Battarbee *et al.*, 2002; Beniston, 2003).

Biotic communities of high mountain lakes are controlled mainly by direct and indirect climatic forcing factors, such as long ice-cover period and low water temperature (Ohrendorf *et al.*, 2000; Karlsson *et al.*, 2005; Thompson *et al.*, 2005) that impact metabolism and habitat quality, and consequently aquatic biodiversity. Due to the extremity in climatic and limnological conditions and geographic isolation, these aquatic ecosystems have relatively simple food-web structures and low number of species, which are adapted to the extreme environmental conditions (*e.g.*, high UV radiation and short open-water season) or are endemic to the mountain regions (Manca *et al.*, 1998; Van Damme and Eggermont, 2011). Crustacean cladocerans are an important part of aquatic food-webs at high altitude lakes, inhabiting both planktonic and benthic habitats and acting as grazers and detritivores, thus playing a key role in the functioning of alpine lakes. The chitinized exoskeletal body parts of these microcrustaceans preserve in lake sediments as fossils and allow the reconstruction of past community structures and characters in paleolimnological down-core studies (Frey, 1960; Korhola and Rautio, 2001; Rautio and Nevalainen, 2013). Such paleolimnological investigations based on subfossil Cladocera have provided important insights on long-term

ecosystem dynamics in sensitive alpine lakes (Hofmann, 2000; Manca and Comoli, 2004; Nevalainen *et al.*, 2014), providing evidence for the major role of atmospheric control, whether direct or indirect, in structuring high altitude cladoceran communities. Under the post-industrial period from ~1850 AD onward, even most of the remotest regions of the world have been affected by atmospheric pollution and climate warming, as this has been demonstrated by paleolimnological studies (Smol *et al.*, 2005; Lami *et al.*, 2010). The Himalayas, which is the highest and largest mountain range of the world and located in the south-central part of the large Asian continent, has provided intriguing possibilities to investigate global environmental change phenomena, such as transport of pollutants and recent climate warming and their effects on lake ecosystems (Baudo *et al.*, 2007; Lami *et al.*, 2010). Since high altitude lakes of the Himalayas are closely coupled with atmospheric processes, their fauna and flora have been shown to respond sensitively to past and present climate changes (Guilizzoni *et al.*, 1998; Lami *et al.*, 1998, 2010; Manca and Comoli, 2004).

Cladoceran distribution in high altitude sites in the Himalayas has been previously described by Manca *et al.* (1994), who reported the occurrence of eight cladoceran species (three Daphniidae, four Chydoridae, one Machrothricidae) in lakes in the Mount Everest-Sagarmatha National Park, Khumbu Himalayan Region in Eastern Nepal. A melanized *Daphnia (Ctenodaphnia)* was synonymized as *D. fusca* Gurney 1907 (Benzie, 2005), while a pale *Daphnia longispina gr.* was identified as *D. dentifera* Forbes 1891 by molecular markers (Möst *et al.*, 2013). In addition, melanic *Chydorus sphaericus* Müller 1776 type specimens were abundant (Manca *et al.*, 1994). Cladoceran fossils have also been utilized in examining long-term community succession in the Khumbu region revealing unique aquatic and sedimentary environments, where *Daphnia* headshields have been preserved abundantly as fossil remains, and where past climatic changes have dictated limnological conditions affecting cladoceran communities and phenotypic properties (Manca *et al*., 1999; Manca and Comoli, 2004). To add knowledge on species distribution of Cladocera and their past environmental responses in the Himalayas, we investigated a 2500-year sedimentary record of fossil Cladocera from Lake Piramide Inferiore (5067 m asl) located in the Khumbu Valley. Our specific aims were to disentangle the historical occurrence of cladoceran taxa and evaluate community responses to previously established paleoclimatic- and limnological regimes. The unique physical environment (*e.g.*, long ice-cover period, low temperature, high UV radiation) and low anthropogenic pressure of the examined mountain summit lake, together with the paleolimnological approach of long-term ecosystem observations, allow interpretations on the ecological sensitivity and distribution of Cladocera in mountain lakes under past and ongoing environmental changes.

METHODS

Lake Piramide Inferiore (LPI; 27°57'45''N; 86°48'56''E, surface area 1.67 ha; maximum depth 14.8 m) is located in the Mount Everest-Sagarmatha National Park, Eastern Nepal, Khumbu Himalayan Region (Fig. 1a). The lake is lying at an altitude of 5067 m asl, and is part of a cascade system receiving water from the upper Lake

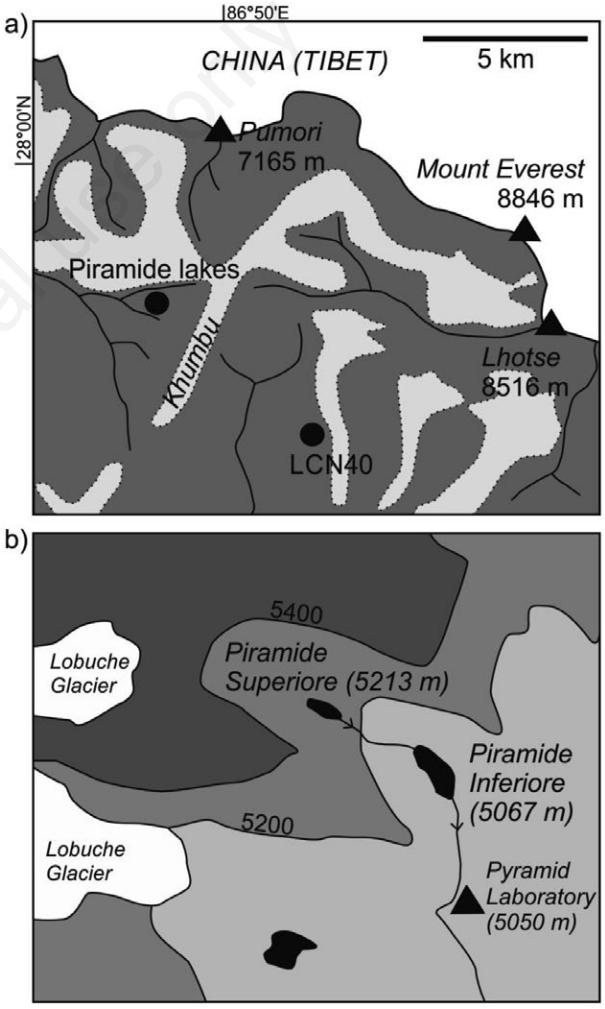

Fig. 1. a) Location of the Piramide lakes (and LCN40) in northeastern Sagarmatha National Park, Himalayan mountain range, Nepal; light gray areas with dashed lines indicate glaciers, black lines mountain summits, and triangles high mountain peaks. b) Location of the Piramide lakes (black areas) and the Pyramid Laboratory (triangle) in Khumbu Valley; different shades of gray from light to dark indicate altitudinal differences (<5200 m, 5200-5400 m, and >5400 m, respectively).

Piramide Superiore (5213 m asl, Fig. 1b). Both lakes are named after the Ev-K2-CNR laboratory (the *Pyramid*; http://www.share-everest.org), established in 1990 on the Nepalese side of Mount Everest in the Sagarmatha National Park for environmental and medical monitoring and research and they represent lake cadastre numbers (LCN) 10 (Piramide Inferiore) and 9 (Piramide Superiore) according to Tartari *et al.* (1998).

LPI is ice-covered for 9-10 months per year, from October-November to June-July and it is ultraoligotrophic with chlorophyll *a* concentration <1 µg L^{-1} (Guilizzoni *et al.*, 1998), total phosphorus ~2.6 µg L^{-1}, and dissolved organic carbon (DOC) ~0.5 mg L^{-1} (Lami *et al.*, 2010). The water column of the lake is highly transparent due to low DOC concentrations; Secchi depth is 14.5 m, approximately same as the maximum depth (Manca *et al*., 1994) and 1% attenuation depth of UV radiation at 320 nm is 7.8 m (Sommaruga, 2010). The cold and semi-arid climate of the region is controlled by the Asian monsoon and high altitudinal location. Meteorological observations of the Pyramid Laboratory-Observatory indicate that mean annual temperature is -2.5°C and mean summer (June-September) temperature is typically above 0°C (Lami *et al.*, 2010). The coldest month is usually February, while the warmest is July. Total annual precipitation is ~520 mm and most of the precipitation occurs during summer months.

A sediment core (LPI1/93) of 69 cm length was collected in 1993 near the deepest zone of LPI with a gravity corer (Plexiglas tube, 6 cm diameter). The core was vertically cut and sectioned into 1-cm slices. One half was used for describing the sediment structure and lithology, as well as for dating, the other was used for analyzing Cladocera remains. The core was dated using ^{210}Pb and ^{14}C dating method and an age-depth model was created resulting in base-of-the-core age of *ca.* 2500 cal yr BP (Lami *et al.*, 1998). Results on fossil pigments, diatoms, and basic sediment geochemistry are published by Guilizzoni *et al.* (1998) and Lami *et al.* (1998). Frey's (1986) method was used to analyze fossil Cladocera remains. An accurately weighted amount of wet sediment, generally about 3 g, was deflocculated in warm 10% KOH for 2 hs and then rinsed in distilled water through a 40 µm sieve. The material retained by the filter was examined under a microscope at magnifications between 400x and 600x and the number of most abundant body part was used as a measure of abundance for each taxa. Cladoceran data were expressed as relative taxon abundances (% of the total Cladocera community) and concentrations of cladoceran exuviae (number g^{-1} DM). Attribution of *Daphnia* spp. remains (headshields and postabdomens) to *Daphnia* (*Ctenodaphnia*) *fusca* Gurney, 1907 and *Daphnia* (*Daphnia*) *dentifera* Forbes, 1893 was based on detailed morphology of the remains (headshields, postabdominal claws, ephippia). Distinction between the two was based on the diagnostic traits of the two subgenera (Benzie, 2005; Manca *et al*., 1999; Manca and Comoli, 2004) within *Daphnia* genus, *i.e.* differences in headshields, resulting from differences in the dorsocephalic suture and fornices, and in position of the nuchal organ; different structure of ephippium for both, shape and orientation of the egg chambers. The modern occurrence of intact *Daphnia* specimens in the studied lake and in the adjacent region was additionally used as a reference for the fossil identification (Manca *et al*., 1998, 2006; Manca and Comoli, 2004; Möst *et al*., 2013). Identification of *Alona* cf. *guttata* remains to *Alona werestschagini* Sinev 1999 was based on morphological characteristics of postabdomens, which resembled those of *A. guttata,* but contained higher number of marginal denticles, convex dorsal margin, and larger size (Sinev, 1999; Sarmaja-Korjonen and Sinev, 2008), and on previous notes and suggestions on the species distribution in mountain ranges of central Asia (Sinev, 1999; Belyaeva, 2003; Glushchenko *et al.*, 2009). Accordingly, in the current study *Daphnia* (*Ctenodaphnia*) remains are addressed as *D. fusca, D. longispina* group remains as *D. dentifera*, and *Alona* cf. *guttata* remains as *A. werestschagini*. Remains of the *Chydorus sphaericus* group are addressed as *C.* cf. *sphaericus* (Szeroczyńska and Sarmaja-Korjonen, 2007).

Estimates of lake productivity and paleoclimatic periods were derived from fossil pigments including chlorophyll derivatives (CD), total carotenoids (TC) and pheoforbides, and sediment organic matter (OM) that were originally presented by Lami *et al.* (1998). Pearson's correlations between the cladoceran data and the proxy data were calculated in the program PAST (Hammer *et al.*, 2001). Relative abundances of species with >3 occurrences in the LPI sediment core were used in principal component analysis (PCA) with the environmental data (CD, TC, pheoforbides, OM) to illustrate inter-species and inter-sample relationships throughout the core. Species data were square-root transformed to stabilize the variance and the data were centered by species. PCA was run with Canoco 4.52 software (ter Braak and Šmilauer, 2002).

RESULTS

Eight Cladocera taxa were encountered from the sediment profile of LPI, of which two were Daphniidae and six Chydoridae. The assemblages were dominated by *Chydorus* cf. *sphaericus* (Fig. 2), which was the most abundant taxon in all the samples having a minimum relative abundance of 80% (~1200 AD) and a maximum of 100% (~500 AD). *Daphnia dentifera* was present in the oldest samples with low abundances but it re-appeared in the stratigraphy and increased around 1200 AD. *Daphnia fusca* occurred in the stratigraphy between 500 BC and 500 AD and again during the topmost part of the core (20th century). *Alona werestschagini* was almost constantly

present in the samples with low abundances with the exception of mid-core samples (~600-900 AD). The less abundant taxa, *Alona* sp. (4 occurrences), *Alonopsis elongata* (Sars, 1861) (1 occurrence), *Leydigia leydigi* (Schoedler, 1863) (1 occurrence), and *Pleuroxus* sp. (3 occurrences), appeared rarely in the upper half of the core (33.5-0.5 cm). The lowest concentration of cladoceran exuviae was at 26.5 cm (~1200 AD, 121 exuviae) and the highest at 54.5 cm (~0 AD, 163,367 exuviae) (Fig. 2).

The PCA resulted in eigenvalues of 0.681 for axis 1 and 0.159 for axis 2. In the PCA of species, samples and environmental variables, *C.* cf. *sphaericus* and *D. fusca* were associated with negative PCA axis 1 values (and high TC, CD, and OM values) and *D. dentifera* and *A. werestschagini* with positive scores (Fig. 3). The sample scores were scattered in the PCA ordination without any specific stratigraphic orientation, with the exception of some samples of warm climate periods, which had mostly negative scores (Fig. 3). The PCA axis 1 sample scores varied between -1.0 and 3.7 (Fig. 2) and there was a slight decrease toward negative values from the bottom samples of the core until ~500 AD. Around 1000 AD the sample scores were more positive but varied to a large extend until the topcore (Fig. 2). PCA axis 1 scores and cladoceran exuviae concentrations correlated significantly ($P<0.05$) with TC ($r=-0.46$ and 0.61, respectively) and OM ($r=-0.35$ and 0.58). *Daphnia* (*D. dentifera* and *D.*

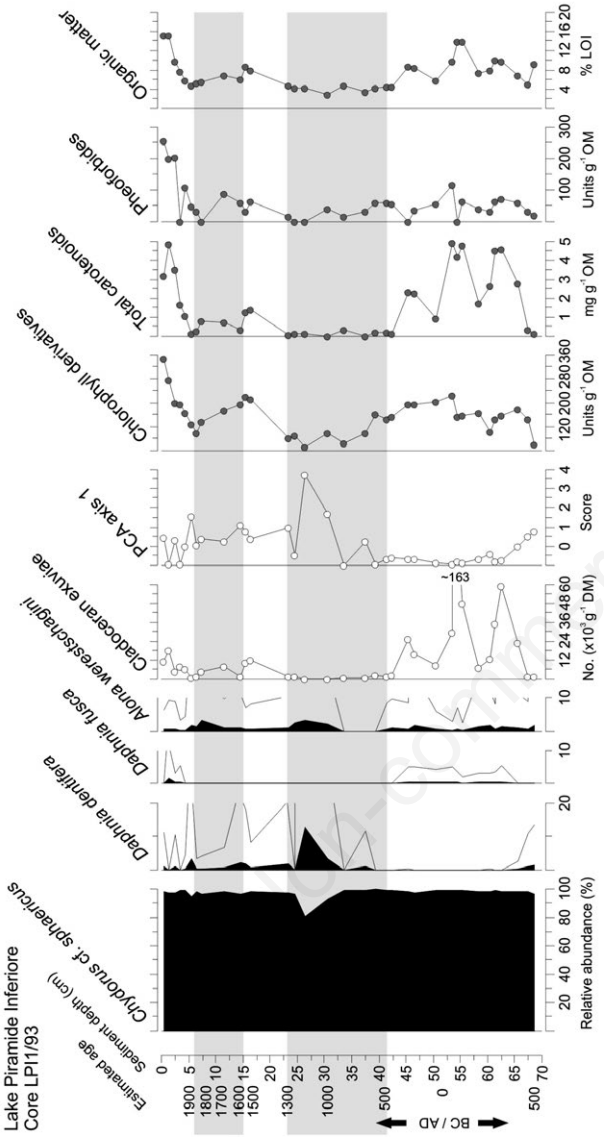

Fig. 2. Relative abundance of cladoceran taxa (>3 occurrences with 10 x exaggeration silhouette), total concentration of cladoceran exuviae, and PCA axis 1 scores along the sediment profile of Lake Piramide Inferiore. Fossil pigments (chlorophyll derivates, total carotenoids, and pheoforbides) and organic matter, originally presented by Lami *et al.* (1998), are also shown. Stratigraphic periods with gray background shading indicate cold climate phases according to pigment and diatom data by Lami *et al.* (1998) from the same sediment core (LPI1/93). Individual sample depths (shown as white and gray dots) are the same for all diagrams.

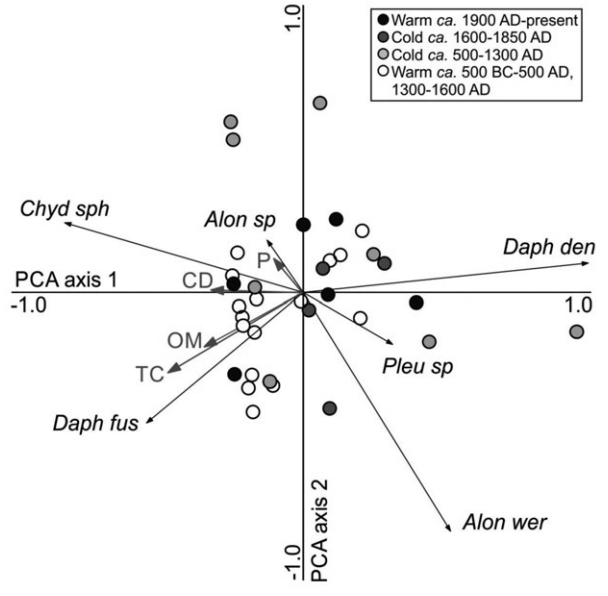

Fig. 3. Principal component analysis (PCA) ordination of cladocera taxa (black arrows; four letters from the genus and three from the species name) and samples (dots) in the sediment core of Lake Piramide Inferiore along first ($\lambda=0.681$) and second ($\lambda=0.159$) PCA axes. Chlorophyll derivates (CD), total carotenoids (TC), pheoforbides (P) and organic matter (OM) were included as environmental variables (gray arrows) and are originally presented by Lami *et al.* (1998), whom also the paleoclimatic periods follow.

fusca) relative abundances did not have significant relationships with the productivity proxies, whereas *Daphnia* concentrations correlated with CD (r=0.33), TC (r=0.68), and OM (r=0.70) (Tab. 1).

DISCUSSION

Notes on species occurrences

The current examination of the LPI sediment core revealed that the lake has been inhabited through the 2500-year period by eight cladoceran taxa of which four (*Daphnia dentifera*, *Chydorus* cf. *sphaericus*, *Alona werestschagini*, and *Alona* sp.) were found from the topmost sediment section, representative of the present community. However, contemporary zooplankton sampling (samples collected once in 1992) of LPI suggested that also *Daphnia fusca,* which was synonymized with *D. tibetana* by Benzie (2005), inhabited Lake Piramide Inferiore (Manca *et al.*, 1994). Sampling of the lake during later years (six sampling dates in 1993, singles in 1994, 1997, 2010) did not record the occurrence of *D. fusca* anymore but instead *D. dentifera*, synonymized with *D. longispina* var. *aspina* by Möst *et al.* (2013), was the sole and dominant *Daphnia* species present in LPI (Manca *et al*., 1998; Sommaruga, 2010). In addition, chydorids *C. sphaericus* and *Alona rectangula* occurred in these latter zooplankton samples by Manca *et al.* (1998). The previous zooplankton survey of 19 lakes (including LPI) located in the Mount Everest-Sagarmatha National park indicated the presence of two *Daphnia* species in the regions: the melanic *D. fusca* and the non-melanic *D. dentifera* (Manca *et al.*, 1998). Additionally, melanic *Simocephalus vetulus,* four chydorid taxa *Alona rectangula, Acroperus harpae, Chydorus sphaericus* (melanic) and *Chydorus* sp., and *Macrothrix hirsuticornis* were recorded from the region. In a different survey from the same region also *A. guttata* was reported (Manca *et al*., 1994). Manca and Comoli (2004) studied a sediment core from a nearby lake (LCN 40, Fig. 1a) covering the past 3000 years and observed that chydorids (*C. sphaericus, A. guttata*, and *Alona rustica*) dominated through the core, while *Ctenodaphnia* persisted as the only *Daphnia* species until the late 1980s after which it was replaced by the species of the *D. longispina* group.

The current results showed a clear, through-core dominance of the *Chydorus* cf. *sphaericus* as it comprised 80-100% of the cladoceran community during the past 2500 years (Fig. 2). Although *Chydorus sphaericus sensu stricto* is previously reported from Nepal as intact specimens (Dumont and Van de Velde, 1977; Manca *et al.*, 1998), the identification of specimens may be inaccurate due to the fact that the species is presently characterized as a cryptic species complex by molecular means and morphological attributes of sexual stages (Belyeva and Taylor, 2009). Furthermore, the identification of *C. sphaericus* remains is usually coarse since the morphological and molecular features needed for precise identification vanish through time in the sediments (cf. Szeroczyńska and Sarmaja-Korjonen, 2007; Belyeva and Taylor, 2009). It is likely that *C.* cf. *sphaericus* in the LPI sediment core was throughout the same species, most likely highly adapted to the extremity of the high altitude environment *e.g.* through pigmentation (cf. Manca *et al.*, 1998). The long-term dominance of *C. sphaericus* type over other cladoceran taxa has also been previously recorded from the Khumbu region (Manca and Comoli, 2004, LCN 40) and other climatically severe regions, *e.g.* from arctic Svalbard (Guilizzoni *et al.*, 2006; Luoto *et al*., 2011) and Canada (Luoto *et al.*, 2013).

Another chydorid, which occurred temporarily with a slightly higher abundance (maximum 3.5% at 26.5 cm) in the LPI sediment core, was *Alona* cf. *guttata* that was attributed to *Alona werestschagini* in the present record (Fig. 2). This taxon was present in LPI almost constantly with the exception of period *ca.* 600-900 AD. The species belongs to the complex *Alona guttata* group, it has been described from Kirghizia (type locality) and Russia, and it has a wide but patchy distribution in Eurasia (Sinev, 1999). It has additionally been recorded from northernmost European Russia (Sinev, 1999, 2002), mountain ranges (Pamir, Tien Shan, Altai, Sayan) of the central Asia (Sinev, 1999; Belyaeva, 2003; Glushchenko *et al.*, 2009) and from northern Scandinavia in Norway (Walseng *et al.*, 2006) and Finland (Sarmaja-Korjonen and Sinev, 2008; Nevalainen, 2009). Based on the earlier records of its occurrence, the distribution of *A. werestschagini* could extend to Himalayas. *A. werestschagini* can be characterized as an in-

Tab. 1. Pearson's correlations between cladoceran-based indices (PCA axis 1, exuviae concentration, and *Daphnia* relative abundance and concentration) and fossil algal pigments and organic matter in the sediment profile from Lake Piramide Inferiore.

	PCA1	Total exuviae	*Daphnia*, %	*Daphnia* exuviae
Chlorophyll derivates	-0.32	0.12	-0.29	0.33*
Total carotenoids	-0.46*	0.61*	-0.23	0.68*
Pheoforbides	-0.10	-0.07	-0.11	0.14
Organic matter	-0.35*	0.58*	-0.21	0.70*

**Significant (P<0.05) correlations.*

habitant of oligotrophic waters of cold climates in high altitude and latitude regions of the Palearctic. It is suggested to be a glacial relict species that may have had a wider distribution in Eurasia during the last glacial period (Sarmaja-Korjonen and Sinev, 2008). The fact that *A. werestschagini* type remains were found in the topmost sediment section (Fig. 2) implies that the species may have inhabited the lake at the time of sampling, although the very low abundance of its remains (0.6%) suggested that it was rare and therefore not retrieved during the zooplankton collections (Manca *et al.*, 1998). Nevertheless, this is the first record of the species in the Himalayas, although caution should be used when addressing species modern distribution based on fossil remains due to the lack of the morphological characteristics (*e.g.*, trunk limbs) used in original taxonomic descriptions (intact specimens).

According to the data from fossil specimens of the surface sediment layer, the prevalent *Daphnia* species in LPI is currently the non-melanic *D. dentifera* of the *D. longispina* group, as it replaced the melanic *D. fusca* in the topmost sample (Fig. 2). In agreement, *D. dentifera* was recorded from the water column of the lake (Manca *et al*., 1998; Sommaruga, 2010; Möst *et al*., 2013). As discussed above, *D. fusca* was reported in the zooplankton samples of LPI in 1992 (Manca *et al.*, 1994) but not after that (in 1993-94, 1997, or 2010) (Manca *et al*., 1998; Sommaruga, 2010; Möst *et al*., 2013), being in accordance with the surface sediment data. A similar phenomenon, the disappearance and total replacement of the melanic *Ctenodaphnia* by the non-melanic *D. longispina* group species, occurred also in the adjacent LCN 40 (Manca *et al.*, 1999; Manca and Comoli, 2004). The 2500-year sediment record of LPI showed a periodic success of the melanic and non-melanic *Daphnia*; *D. fusca* was prevalent, although not abundant (ca. 0.3-0.5%), during the lower part of the core (~500 BC-500 AD) and during the 20th century, whereas *D. dentifera* reappeared in ~500 AD after a thousand years pause and increased up to ~10% between 1000 and 1300 AD inhabiting the lake until the 20th century (Fig. 2). It appears that these two taxa had only very short periods of co-occurrence (at depths 60.5, 45.5, and 2.5 cm) and otherwise only one of them was the sole planktonic taxon in the lake, although the extremely low abundance of cladoceran remains in the LPI core may have resulted in a rarefaction effect where species' presence cannot be verified.

Even though taxonomic resolution in identification of fossil Cladocera is not as high as in studies focusing on contemporary specimens, palaeolimnological studies have recognized rare and even completely new taxa (Sarmaja-Korjonen *et al.*, 2000; Sarmaja-Korjonen, 2005; Nevalainen *et al.*, 2012) and taxonomic resolution of the identification is enhancing (Korosi *et al.*, 2011). Thus, investigations on fossil specimens from surface sediments (representing modern taxa assemblage) or from sediment cores with high temporal range (representing past communities) from wide geographical scales provide invaluable information on cladoceran biogeography and species distribution (Nevalainen *et al.*, 2013). The knowledge of where specific cladoceran taxa live, when and at which abundance, and why they are present or absent in a certain geographical areas are of high importance in understanding collectively species distributional ranges and responses to environmental change throughout the past and at present. However, when addressing species' identities and presence based on sediment samples and fossil remains, caution should be used in identification and evaluating rarefaction effects. Furthermore, the findings should be verified with contemporary sampling, as in the case of *A. werestschagini* presence in LPI (Fig. 2).

Paleoecological implications

In the previous sediment study from LPI, Lami *et al.* (1998) recognized several cold and warm periods for the area during the past millennia based on qualitative pigment and diatom data (Fig. 2). These paleoclimatic inferences were based on the assumption that due to direct correlation between pigment concentrations in sediment and primary production, algal production can be inferred from pigment concentrations (Guilizzoni *et al.*, 1983; Leavitt, 1993) and that increased lake productivity is a consequence of warming climate and increased ice-free period in high altitude lakes where atmospheric control on lakes limnology is strong (Lami *et al*., 2010). Concerning the present study, the paleoclimatic records of Lami *et al.* (1998) are in good agreement with glacier fluctuations in the Himalayas and Karakorum (Röthlisberger and Geyh, 1985; Smiraglia, 1998).

Chlorophyll derivates and total carotenoids, which were highest in LPI core during 500 BC-500 AD and the 20th century (Fig. 2), are indicative of total algal biomass and the overall pigment data suggests that, despite the oligotrophic nature of the lake, periphytic and epipelic algal production was high throughout the core and especially during the warm climate periods (Lami *et al*., 1998). Benthic primary production is typical for transparent lakes located in extremely cold climates where it may predominate over pelagic production supporting pelagic grazers (Rautio and Vincent, 2006). Cladoceran community shifts (PCA axis 1 scores) and exuviae concentrations through the LPI core correlated significantly with total carotenoid concentrations and organic matter (Tab. 1) and the stratigraphic distributions of *D. fusca* and *C.* cf. *sphaericus* were linked with samples of higher algal pigments and organic matter (Fig. 3). The opposite PCA scores, associated with samples of lower productivity, occurred in *D. dentifera* and *A. werestaschagini* (Fig. 3). However, the PCA results and the reliability of the species-environment relationships may have

been hampered by the low species richness and high dominance of *C.* cf. *sphaericus*. *Daphnia*'s relative abundances showed no correlation with the productivity proxies but concentrations of *Daphnia* exuviae correlated positively with chlorophyll derivates, carotenoids and, organic matter (Tab. 1) and may have been controlled by bottom-up mechanisms of algal production. However, the concentration data used should be assessed with caution due to altering sedimentation processes.

Accordingly, it is possible that cladoceran species succession in LPI was driven partly by bottom-up mechanisms through benthic algal communities, which were mainly forced by the regional climatic oscillation (Lami *et al*., 1998, 2010). In fact, chydorids are mostly affiliated with benthic habitats (bottom substrata and vegetation) and *Daphnia* in these transparent mountain lakes is known to thrive near the bottom among benthic mosses and filamentous algae seeking for a UV refuge (Manca *et al.*, 1994, 1998). Sedimentary pheoforbides are indicative of zooplankton grazing and may give insights on changes in zooplankton assemblages and their size distribution under altered food web conditions (Carpenter *et al.*, 1988) but cladoceran community changes or *Daphnia* abundances did not correlate with this measure in the LPI core (Tab. 1). Based on the assumption that cladoceran communities respond to long-term bottom-up and top-down drivers in aquatic food webs (*e.g.* Perga *et al.*, 2010), changes in aquatic invertebrate predators in LPI may have impacted the observed millennia-long community succession. The lake is currently inhabited by a copepod *Arctodiaptomus jurisovitchi* (Manca *et al*., 1998; Sommaruga, 2010) that can feed on cladoceran eggs, similarly to what has been found for cyclopoid copepods (Gliwicz and Stibor, 1993; Manca and Comoli, 1999), and it may have caused significant changes in cladoceran assemblages by negatively affecting their reproduction. However, we do not have knowledge on the historical occurrence of *Arctodiaptomus* in LPI and therefore cannot evaluate the top-down controls further. In addition, impact of *Daphnia* micro-parasites is often overlooked (Manca *et al*., 2007; Wolinska *et al*., 2007).

In the topcore, during the late 20th century, algal pigments and organic matter increased clearly (Fig. 2) and additionally, Lami *et al*. (1998) report a recent increase of total organic carbon and Guilizzoni *et al.* (1998) that of total sediment phosphorus in LPI. Considering these facts, cladoceran response to the recent environmental changes (inferred as increased lake production linked to climate warming) was subtle, however, including the reappearance of *D. fusca* into the stratigraphy following a millennium of its absence. In addition to the climatically-mediated primary production, which presumably increased and is correlated with altered algal communities (Lami *et al*., 2010), more intense UV radiation may have favored the recent short-term establishment of the melanic *Daphnia fusca* population in LPI (Rautio and Korhola, 2002). However, as stated above, *D. fusca* is currently absent from the lake and the lake is inhabited by the pale *Daphnia.*

Long-term Daphnia-Ctenodaphnia dynamics

The consecutive success of *D. dentifera* and *D. fusca* throughout the past two millennia in LPI is intriguing. LPI is the lower lake of a cascading system of the two Piramide lakes and currently the upper Piramide Superiore (Fig. 1) is permanently inhabited by the melanic *D. fusca* (synonym for *D. himalaya* in Peñalva-Arana and Manca, 2007; Sommaruga, 2010), whereas the recent occurrence of the taxon in the lower Piramide Inferiore exhibited short-term variations and it does not inhabit the lake currently (see discussion above and Fig. 2). Thus, it is possible that, in the absence of a permanent *D. fusca* egg bank in the sediments of LPI (Piscia *et al.*, 2006; Manca, 2009), the upper lake may have acted as a biotic reservoir for this taxon. If such would be the case, periods of *D. fusca* occurrence in the LPI sediment profile might then be indicative of periods of higher connectivity between the two lakes (*i.e*., increased precipitation). Lami *et al.* (2010) suggested, based on a core taken in 2002, that there was a pronounced decrease in LPI lake level at ca. 500 AD and accordingly, if the succession of *D. fusca* was related to periods of higher connectivity between the upper and lower Piramide lakes, its decrease and disappearance from the LPI core around 500 AD could have been impacted by decreased effective moisture and disconnection of the two lakes due to lower water tables (Figs. 1 and 2). Further factors contributing to the periodic *D. fusca* and *D. dentifera* dynamics in LPI may include differing physiological functions of *Daphnia* juveniles in the oligotrophic and low conductivity lakes. It has been shown that early instar *D. fusca* specimens found from the Khumbu region maintain the nuchal organ longer than *Ctenodaphnia* taxa from other environments (Manca *et al.*, 1999; Peñalva-Arana and Manca, 2007); such organ is used for osmoregulation in low-conductivity lakes. It was suggested by Peñalva-Arana and Manca (2007) that precipitation and subsequent ground water inflow are the main sources of ions for the *Ctenodaphnia* lakes, making them extremely low in ionic composition and explaining the osmoregulation requirements and taxon success in these particular systems. Thus, the temporal replacement of *D. dentifera* by the *D. fusca* in LPI (Fig. 2) may be linked to fluctuating ionic input in a way that *D. fusca* was favored under periods of low ionic content. Lami *et al.* (2010) indicated that ionic content of LPI has increased since the early 1990s. They linked this change with increasing air temperatures and proposed that longer ice-free season and unfrozen soils enhance chemical weathering and as a consequence, increase the input of weathering products to lake water. This situation may have favored *D. denti-*

fera during the recent decades in LPI (Lami *et al*., 2010; Fig. 2) but it does not seem to fit with the millennial cladoceran record, since *D. fusca* prevailed during warm climatic periods of ~500 BC-500 AD and the 20th century.

As stated above, *D. fusca* and *D. dentifera* rarely co-occur in space and time and they differ from each other most importantly with the pigmentation of their carapaces; the former is strongly melanized having completely dark carapaces (Manca *et al*., 2006; Sommaruga, 2010) and the latter is pale without any carapace melanin and only pigmented ephippia (Sommaruga, 2010; Möst *et al*., 2013). The mountain lakes of the Khumbu region, which are not directly connected to glaciers, are highly transparent and are exposed to deep underwater UV penetration (Sommaruga, 2010) affecting biota negatively. Therefore, the differences in carapace pigmentation are likely related to adaptive strategies of the taxa to cope with high UV exposure and this environmental response may explain *Daphnia* dynamics in the LPI core (Fig. 2). Under this context, the occurrence of *D. fusca* could be associated with periods of higher UV exposure and *D. dentifera* to lower UV exposure.

The proxy data of algal pigments showed that melanic *D. fusca* was linked with periods of higher algal production and climate amelioration (Figs. 2 and 3) during ca. 500 BC-500 AD and the 20th century. Consequently, the presence of the *Daphnia* species with melanized carapaces may suggest that the lake exhibited high UV exposure. On the opposite, *D. dentifera* occurred during periods of reduced productivity and colder climate (Fig. 2 and 3) suggesting lower UV exposure. The duration of ice-cover period and timing of ice breakage in spring are known to have significant impacts on the underwater UV exposure in alpine lakes (Vincent *et al*., 2007) and *Daphnia* are known to respond to this peak radiation period by melanin synthesis (Rautio and Korhola, 2002). Accordingly, it is possible that the *Daphnia* dynamics in LPI were forced by climate-driven changes in duration of ice-cover that would have changed underwater UV regimes. Then, warmer climate could have induced higher underwater UV exposure during the spring and open-water season and the success of melanic *D. fusca* and cooler climate could have resulted in less intense UV radiation and the success of non-melanic *D. dentifera* (Fig. 2) during the sensitive summer period of hatching, growth, and reproduction affecting species occurrences (Gliwicz *et al.*, 2001).

In the previous fossil cladoceran record from the Khumbu region (LCN 40 in Fig. 1; Manca and Comoli, 2004), the 3000-year cladoceran history was dominated by the melanic *D. fusca* and the non-melanic *D. dentifera* established a population during the late 1980s. The recent success of the pale *Daphnia* was attributed to increased photoprotective properties of the water column (*i.e*., increase in algal production and organic carbon) reducing UV radiation exposure contradictory to the presumption that recently increased UV irradiance would affect negatively non-pigmented taxa (Rautio and Korhola, 2002). However, despite the clear long-term periodic success of the melanic and non-melanic *Daphnia* in LPI, the record was not as clear as in LCN 40 where the non-melanic taxon overtook the melanic species abruptly (Manca *et al*., 1999). In addition, there occurred short-term variation among the species in LPI during the 20th century and 1990s (Manca *et al.*, 1994, 1998; Fig. 2) and these recent dynamics cannot be directly linked with the late 20th century UV radiation increase.

According to Möst *et al.* (2013), high lake depth and low total phosphorus were the strongest predictors for the occurrence of pale *D. longispina* group individuals in the Himalayas. High lake depth favors the pale *Daphnia* because it is able to seek deep-water refugia near the bottom, but its relationship with phosphorus remains puzzling, although species of the *D. longispina* group may have a competitive advantage under ultraoligotrophic conditions (Möst *et al*., 2013). In the light of this, the long-term *Daphnia-Ctenodaphnia* dynamics may have additionally been related to lake productivity and bottom-up drivers. Since the long-term *D. dentifera* and *D. fusca* distributions in LPI indicate association of the former with low and the latter with high algal pigment concentrations (Fig. 3), the fossil records seems to be in accordance with the contemporary ecological preferences. However, Möst *et al.* (2013) further suggested that the encounter of the melanic and pale *Daphnia* taxa does not necessarily lead to competitive exclusion allowing them rarely to co-occur. Nevertheless, when combining the existing information on the modern distribution of the two *Daphnia* taxa in the Khumbu region (*i.e.*, that they only occasionally co-occur) with the current paleolimnological record of LPI (Figs. 2 and 3) and the previous investigation from LCN 40 (Manca *et al*., 1999; Manca and Comoli, 2004), it appears that these taxa may actually be ecological counterparts thriving only in specific environmental condition or even excluding each other from ecosystems by competition.

CONCLUSIONS

The community succession of Cladocera and concentration of their remains in LPI were in general agreement with the paleoproductivity proxies suggesting that bottom-up mechanisms have structured the community, although strong correlations were found only with total carotenoid content. In common with other records from cold climate regions, the sediment core revealed a fossil cladoceran record that was dominated by *Chydorus* cf. *sphaericus*. *Alona werestschagini* was recorded for the first time from the Himalayas, as it inhabited the lake almost throughout the 2500-year record, but further contemporary studies are needed to verify its occurrence in

the Khumbu region and the Himalayan mountain range in general. Distinctive long-term dynamics were recognized in the success of two prevalent *Daphnia* species (melanic *D. fusca* and non-melanic *D. dentifera*) during the late Holocene and this succession was most likely related to changes in underwater UV radiation regimes, since they differ from each other significantly with carapace melanization. The results indicate that fossil cladoceran analysis may be used as a useful tool in biogeographical research, revealing species' distributions in space and time. Furthermore, the inclusion of fossil cladoceran records, *e.g.* in the case of *Ctenodaphnia-Daphnia* dynamics in the Himalayas, in addressing species' ecological preferences is extremely beneficial for both paleoecologists and zooplankton ecologists.

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